

COMPARATIVE NOTES ON THE LIFE HISTORY OF THE CAROLINA CHICKADEE¹

RICHARD BREWER

A knowledge of the life histories of closely related organisms is basic to understanding their ecological and evolutionary relationships. The Carolina and Black-capped Chickadees (*Parus carolinensis* Audubon and *P. atricapillus* Linnaeus) are sibling species occupying essentially allopatric breeding ranges. Where their ranges are contiguous in western Illinois and eastern Missouri, interbreeding apparently occurs, with the production of a zone in which a large proportion of the birds may be hybrids. This paper presents information on certain aspects of the life history of the Carolina Chickadee, along with comparative material on the Black-capped Chickadee and on a population occurring at the line of contact between these two species.

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PROCEDURE

Field work was conducted from October 1954 to November 1959. Although some supplemental observations were made in Indiana, Michigan, Missouri, North Carolina, Tennessee, and Texas, the principal areas of investigation were the following counties of Illinois: Bond, Champaign, Clinton, Coles, Cumberland, Douglas, Effingham, Fayette, Jackson, Piatt, Randolph, Shelby, Washington, and Williamson. Observations of the population believed to be composed partly of hybrid birds were confined to the areas along the Kaskaskia River around Vandalia (Fayette County), Illinois, and (observations on vocalizations only) areas in St. Louis and Jefferson Counties, Missouri. Specifically, the area in Illinois included in observations of what will be referred to as the Vandalia population was from the level of Wrights Corner south to near the level of Vernon (i.e., from Sec. 28, T. 8 N., R. 2 E. of the St. Elmo quadrangle to Sec. 34, T. 5 N., R. 1 W. of the Vandalia quadrangle).

Only a few birds, all in the breeding season, were marked. Marking was by means of colored airplane dope applied to the tail feathers. Individual recognition of members of mated pairs was usually possible without marking,

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through differences in appearance. Attentiveness data were gathered directly, without use of mechanical recording devices. To allow direct observation of the nest, five nest stubs, including both species and the *Vandalia* population, were treated in the method described by Odum (1941a): a small, square panel was sawed out of the front of the stub and wired in place. It could be removed and replaced for brief observations of eggs or nestlings.

One brood of Carolina Chickadees (on 3 June 1958) and one of Black-capped Chickadees (on 18 June 1958) were brought into the laboratory after sawing off the nest stubs containing them. Each brood was about 13 days past hatching. The stubs were placed in adjacent flight cages. The Carolina Chickadees were left in their own nest stub until they fledged; the Black-capped Chickadees were placed in the by-then-deserted Carolina nest stub for ease of observation. The Carolina Chickadees were hand-fed from the time they were brought in until they were able to feed independently. The Black-capped Chickadees were hand-fed only on the day of collection; after that, one parent which had been trapped with the young but separated from them was introduced into the flight cage and allowed to resume feeding. The food provided was mealworms (*Tenebrio* sp.) and hamburger.

FLOCK FORMATION AND WINTER BEHAVIOR

Within two to three weeks after fledging, young chickadees become independent of their parents. At this time, young from various family groups may form loose aggregations. These aggregations wander about more extensively than during the period of dependence, when the family group stays in a small area on or near the breeding territory. The adults tend to confine their activities to areas on or near their territory for a time but later join or are joined by other birds and begin to move over a larger area.

Dixon (1959), working with Carolina Chickadees in Texas, reported that this species formed small winter flocks with a home range of about 10 acres (Dixon, in litt.). Organization of the flock was hierarchical with resident pairs dominant. Contrasting the situation he observed with conditions reported for the Black-capped Chickadee (Butts, 1931; Odum, 1941a, 1941b, 1942a), Dixon suggested that Carolina Chickadees may possess a stronger pair bond, be less mobile, and form smaller flocks. It seems possible that these apparent differences may be responses to climate and food supply based on traits that are common to the two species. It is clear that in both species winter dominance is related to breeding-season territoriality, dominant birds tending to have breeding territories included in the winter home range (Dixon, 1959; Odum, 1942b; Hamerstrom, 1942). There is no obvious difference in strength of the pair bond, inasmuch as both species tend to pair for life (see "Pair Formation"). Probably flock size, as well as the degree of constancy of flock composition, varies with many factors both of the birds them-

selves and of the environment. For example, Johnston (1942) has pointed out the tendency of Black-capped Chickadee flocks to disperse at temperatures above 25°C. In Illinois, where both species may be found at the same latitudes, mean flock size (considering any group of chickadees encountered in the winter as a flock) for 21 Carolina Chickadee flocks was 3.3 birds (S.E. = 0.253), and for 16 Black-capped Chickadee flocks it was also 3.3 (S.E. = 0.034). Obviously, no significant difference exists between the two means. Mean size for eight flocks of the *Vandalia* population was 3.8 (S.E. = 0.558), which is not significantly different from either parental species. In Illinois, both species appear fairly regularly in twosomes. Laskey (1957) has stated for Carolina Chickadees in Tennessee that these twosomes may be either a mated pair, adult and young, or two young birds.

The winter home range found by Dixon in Texas is small, but Nice (1933) calculated that one pair of Carolina Chickadees in Ohio had a home range of about 35 acres in one winter. This is about the same size as that found for Black-capped Chickadees in New York and Michigan (Butts, 1931; Odum, 1942*b*; Batts, 1957). The observation of Batts that home ranges tend to increase in size as the winter progresses suggests that food may be an important factor in determining their size. If this is true, smaller home ranges in the southern United States might be expected.

In both species of Chickadees (Odum, 1942*a*; Hamerstrom, 1942; Dixon, in litt.), well-defined uni-directional dominance orders are present. Dixon found that in the small flocks on his study areas the relationship was linear, but in the larger assemblages studied by Odum and Hamerstrom, deviations from complete linearity were observed.

Chickadees are often encountered in feeding parties composed of a number of species. These parties often include migrant warblers and vireos in the autumn and spring, and Odum (1942*a*) believed that aggregations with these species are held together by definite social bonds. The parties tend to move as groups, and call notes, particularly alarm notes of chickadees (and titmice) tend to have some integrating action on the other species. From autumn to spring, certain winter and permanent resident birds are frequently associated with chickadees. In Illinois, Tufted Titmice are the most constant associates of chickadees when they form interspecific feeding parties (Table 1). White-breasted Nuthatches, Golden-crowned Kinglets, Brown Creepers, Red-bellied Woodpeckers, and Downy Woodpeckers are also fairly frequent associates.

The temporary nature of these parties, resulting partly from differences between the species in vegetational requirements and in rates of travel, has been commented on by several writers (e.g., Odum, 1942*a*; Fitch, 1958). Butts (1927) stated that Black-capped Chickadees spent about one-sixth of their time in company with White-breasted Nuthatches.

TABLE 1
 OCCURRENCE OF VARIOUS BIRD SPECIES IN 24 FEEDING PARTIES WITH BLACK-CAPPED
 CHICKADEES, 8 FEEDING PARTIES WITH CAROLINA CHICKADEES, AND 5 FEEDING
 PARTIES WITH CHICKADEES OF THE VANDALIA POPULATION¹

Species	Carolina Chickadee		Black-capped Chickadee		Vandalia Population	
	No.	Per cent	No.	Per cent	No.	Per cent
Tufted Titmouse (<i>Parus bicolor</i>)	8	100	20	83	3	60
Downy Woodpecker (<i>Dendrocopos pubescens</i>)	5	62	11	46	2	40
Golden-crowned Kinglet (<i>Regulus satrapa</i>)	3	38	1	4	2	40
White-breasted Nuthatch (<i>Sitta carolinensis</i>)	2	25	17	71	4	80
Red-bellied Woodpecker (<i>Centurus carolinus</i>)	2	25	8	33	2	40
Brown Creeper (<i>Certhia familiaris</i>)	2	25	7	29	3	60
Red-breasted Nuthatch (<i>Sitta canadensis</i>)	1	12	—	—	—	—
American Goldfinch (<i>Spinus tristis</i>)	1	12	—	—	—	—
Hairy Woodpecker (<i>Dendrocopos villosus</i>)	—	—	5	21	—	—
Cardinal (<i>Richmondia cardinalis</i>)	—	—	1	4	—	—
Purple Finch (<i>Carpodacus purpureus</i>)	—	—	1	4	—	—
Yellow-shafted Flicker (<i>Colaptes auratus</i>)	—	—	—	—	1	20

¹ The sample for Black-capped Chickadee includes 15 parties from Johnston (1941).

Fighting. Intraspecific and, when it occurs, interspecific aggressiveness in Carolina and Black-capped Chickadees, whether associated with feeding, territoriality, or other actions, appears to consist of vocalizations, supplanting attacks, chasing, and actual combat. Aggressive vocalizations are discussed in a later section. Combat generally occurs in the air when a bird resists a supplanting attack or a chase. Combat is similar in the two species and resembles that described by Hinde (1952) in the Great Tit (*Parus major*). The two birds face each other with bodies upright, flail with their wings, and strike with beak and claws. The birds may fall to the ground, and one may withdraw or there may be further supplanting, chasing, or combat.

The variety of aggressive displays reported by Hinde (1952) for the Great Tit either are absent or difficult to detect in the two chickadees. Something resembling the wings-raised and head-forward postures are occasionally seen, and Odum (1942a) used what seems to be the head-forward posture as one of his criteria of dominance. These displays seem not to be very

specific; for example, a wounded bird may give what appears to be the head-forward posture to a collector who has cornered the bird in order to dispatch it. It may be that displays as distinct and frequent as were observed by Hinde are merely given more rapidly or are less conspicuous in the smaller chickadees; perhaps study of motion pictures would supply the answer.

PAIR FORMATION

Considerable evidence exists that members of a pair of chickadees remain together after nesting and, if both survive, nest together the following season (*P. carolinensis*: Nice, 1933, Dixon, in litt.; *P. atricapillus*: Baldwin, 1935, Harding, 1942, Odum, 1942*b*). Pair formation, and probably re-affirmation of the pair bond, appears to begin in the flock during early spring. The process seemingly is a gradual one, similar in its general outlines to that described by Hinde (1952) for the Great Tit. Males begin to exhibit increased aggressive behavior. Some birds, presumably females coming into reproductive condition, begin avoiding attacks rather than meeting them or flying, as is the case with other females and males.

Some other elements may be present in the formation of the pair bond. Although Odum (1941*a*) stated that one of the functions of the whistled song is to attract females, I have no definite evidence that it has any role in pair formation. Long flights in which the female follows the male are frequent during the period of separation of pairs from the flock and may have some role in forging the pair bond. It is not clear whether hole inspection and excavation have any part in pair formation. If they do, they come into play only after the two birds have been associated for a time. The following typical example of hole inspection was observed on 1 April 1956, in the Carolina Chickadee, but does not differ appreciably from the same action in Black-capped Chickadees or birds of the Vandalia population. Two birds had been observed feeding 3-20 feet apart for 15 minutes. One flew to a hole in a dead willow (*Salix nigra*).

It looked inside the hole by perching on the side of the trunk, then flew nervously about, perching on vines of poison ivy (*Rhus radicans*) near the hole. It looked inside several times. In about one minute the second chickadee flew up, looked inside the hole and then flew in headfirst. After a few seconds it came out and both flew approximately 60 yards to a soft maple (*Acer saccharinum*) and commenced feeding. About two minutes later one bird came back and looked inside and went in for six to ten seconds. Then it came out and moved away.

Presumably, the first bird was the male and the second was the female.

Once the pair has been formed, the two birds typically continue to range widely, spending most of their time feeding as before. Stumps possessing or suitable for a cavity are inspected and some desultory excavation may be begun. If another pair or another adult is met, a fight may ensue. There is

excited calling, supplanting attacks, chasing, and sometimes combat. Fights during this period are more vigorous than at other seasons. Often, the loud vocalizations attract one or more additional pairs. Fitch (1958) has recorded instances in the Black-capped Chickadee in which eight birds were involved. After several minutes the birds drift apart, but the same actions may be repeated in the same areas (perhaps those most suitable for nesting) several times during a day.

NEST-SITE SELECTION, TERRITORIALITY, EXCAVATION, AND NEST BUILDING

As has been suggested, nest sites are chosen after inspection of several possible locations. Excavation, and even nest-building, may be begun at several sites before the pair concentrates on the cavity in which the eggs will eventually be laid. Some of the sites investigated may be unsuitable. Hinde (1952) has pointed out the adaptive value of being able not only to occupy the best possible sites but also to occupy inferior sites if more suitable ones are unavailable.

If a pair (and perhaps if only one member of the pair) survives from one year to the next, it often shows a tendency to nest in the same cavity, or at least in the same tree it used previously (*P. carolinensis*: Tanner, 1952; *P. atricapillus*: Boyles, 1922; Butts, 1931).

Excavation seems identical in the Carolina and Black-capped Chickadees. Both birds of the pair excavate, often working alternately. The bird not excavating may feed, rest near-by, or sing if it is the male. The female spends much longer periods in the cavity than does the male. At first, the excavating bird perches on the side of the stub. Later it perches on the rim of the hole and, as the hole deepens, goes inside. In the early stages, the bird usually pounds loose several chips and then rears up and discards them with shakes of the head. When the hole is deeper, there is a tendency for the bird to fly some distance (generally 5–20 feet) before discarding the chips. During any one period of a few hours, the perch used for this purpose is the same, but it is changed from time to time. There appears to be an alternation of attentive and inattentive periods during excavation.

A noticeable difference existed in excavation as practiced by the Vandalia birds. At five cavities where I observed excavation for a total of more than 50 minutes, only one bird excavated, and in four instances, it was the female.

In all three populations, occupancy of cavities other than those excavated by the birds themselves is rare. When a pair does make use of a suitable pre-existing cavity, some excavation is nearly always performed, even though this may produce no noticeable improvement in the cavity. Observing that Black-capped Chickadees rarely nest in nest-boxes, Drury (1958) prepared boxes in which the cavity was filled with peat and sawdust. Five of 11 of these

boxes were utilized, whereas none of 25 standard boxes in similar situations was occupied. It is conceivable that excavation is some essential part of courtship, necessary for reaching or maintaining the psychological conditions required for mating. Inasmuch as chickadees do sometimes make use of nest-boxes in which excavation is impossible, the need for excavation may not be absolute or else can be satisfied by excavating at other sites which are not suitable for actual nesting.

The stub used for nesting is usually around 165–200 centimeters in height and 11–13 centimeters in diameter where the hole is placed. Trees with the inner portion softened by decay but with outer layers of wood or bark still firm are usually chosen. The particular species chosen depends on what species satisfy these requirements in any particular geographical region, but willows (*Salix* spp.), pines (*Pinus* spp.), cottonwoods and poplars (*Populus* spp.), and fruit trees of the genera *Pyrus* and *Prunus* are widespread choices.

Excavation may be followed immediately by lining of the cavity, or a period of several days (at least 16 at one nest of the Vandalia population) may ensue during which the cavity is rarely visited. Desultory excavation having no appreciable effect on the size of the cavity may be carried on during this period and also during the early stages of nest-building.

Four measurements were taken of nest cavities as follows: maximum entrance height and width, diameter of cavity at nest level, and depth of cavity from top of entrance hole. These measurements were similar for the three populations except for height of entrance hole (Table 2). The difference of seven millimeters between the larger holes of Black-capped Chickadees and the smaller holes of Carolina Chickadees was significant with a *P* value of less than 0.01. Height of entrance hole in the Vandalia population was intermediate but nearer the size characteristic of the Carolina Chickadee.

During nest-building the female may spend occasional periods merely sitting in the cavity, often in such a position as to look out. This habit may be carried over to some degree into the egg-laying period. In Illinois, nests

TABLE 2
DIMENSIONS (IN MILLIMETERS) OF NESTING CAVITIES OF BLACK-CAPPED AND CAROLINA CHICKADEES AND CHICKADEES OF THE VANDALIA POPULATION

Measurement	Carolina Chickadee		Black-capped Chickadee		Vandalia Population	
	No.	Mean \pm S.E.	No.	Mean \pm S.E.	No.	Mean \pm S.E.
Height of entrance hole	3	40.2 \pm 0.1	3	47.3 \pm 1.4	5	42.0 \pm 1.4
Width of entrance hole	3	44.7 \pm 5.4	3	41.4 \pm 2.7	6	36.7 \pm 1.6
Diameter of cavity	2	65.2	4	64.8 \pm 3.4	2	81.8
Depth of cavity	3	179.0 \pm 18.0	4	199.0 \pm 9.0	4	221.0 \pm 20.2

are most often made of a layer of moss overlain by fine bark strips and lined with fur. The materials are gathered in approximately the same order. A female of the Vandalia population stripped bark from a small branch of a box elder (*Acer negundo*), starting at the base of the branch and working to the tip and then going back on the underside.

The male often accompanies the female as she gathers nesting material but normally gathers no material himself and, although he may enter the cavity occasionally, does not assist in building the nest. Once in the Black-capped Chickadee, I observed a male pick up some fur and transfer it to his mate, and Brackbill (in litt.) observed a male Carolina Chickadee approach the nest with nesting material in its bill, but these are unusual occurrences.

Territorial boundaries appear to be established during the period from the beginning of excavation to egg laying. Odum (1941a) has suggested that territorial defense is an outgrowth of the antagonism of paired birds to other chickadees. Chickadees do not regularly proclaim territories, and territorial use of the whistled song usually occurs only in the early stages of marking out the territory or when an intruder or neighboring bird comes into the territory or near its boundaries. Under these circumstances, vocal duels lasting for several minutes may occur. If close-distance conflicts take place, they appear about the same as fights in any other season. Both sexes may engage in territorial defense, although the male generally takes the initiative. Territorial defense is almost exclusively intraspecific, except that evidence from the contact zone at Vandalia suggests that a pair defends its territory against all other chickadees—Black-capped, Carolina, or hybrid. Available evidence suggests a mean territorial size of about 3.5–4.0 acres, with considerable variation.

MATING AND EGG LAYING

Except that little time is spent around the nest, the behavior of chickadee pairs during egg laying is similar to that during nest building. A pair of Carolina Chickadees either in the egg-laying period or the period of relative inactivity that sometimes follows nest-building was observed from 10:20 AM to 12:20 PM, on 18 April 1957. They fed close together during this time. The female gave the beg call that solicits feeding by the male continually but was fed only about four times. Copulation occurred about noon. The female was near the edge of a riverbottom forest, the male farther in the interior. The male gave a four-noted song and the female flew near him. They perched near one another about 30 feet up and the female shivered her wings. The male appeared to feed the female who continued shivering her wings and flew a few feet to another tree. There, she shivered her wings and spread her wings and tail. The male flew up and perched about three inches from the female and shivered his wings. He called *deedle-up*, flew behind to the female's left, and

mounted briefly. The male and then the female flew off rapidly and resumed feeding.

Copulation apparently is similar in the two species. The following description of copulation between two birds of the *Vandalia* population adds some details to that already given, but does not noticeably differ from it. The observation was made near the end of the nest-building period.

7:55 AM. Female giving *dee-deet-dit* (begging note) about 40 feet up in dead tree. Male giving *fee-bee-febay* and variations. Female shivering wings and flew . . . (to a perch near) male who was perched 22–25 feet up on a small branch of willow. She shivered wings and gave the begging note. Male flew beside her, mounted from left, turned tail over her right side and copulation apparently took place. Female's vent was noticeably expanded or extruded. Male flew off a few feet. Female continued shivering wings a few seconds. Her crown feathers were erect. She stretched wings, shivered briefly, then flew off to west. Male likewise flew west.

Copulation, as well as courtship feeding, probably begins during nest building.

Eggs are laid one a day in the morning, in one case just before the female emerged from the cavity. The female spends the night in the cavity, leaving about sunrise and usually in response to signal songs from the male.

Nesting material, mainly fur, is added to the nest throughout egg-laying. This fur apparently is used to form the flap which typically covers the eggs during this period. The flap appears to be a built-up rear portion of the nest lining which is turned forward over the eggs. The flap may serve two purposes: it conceals the eggs, perhaps making the nest appear empty to a predator, and it may insulate the eggs so that development is not initiated by the female's roosting in the cavity.

Clutch size. Of 63 complete clutches for the Carolina Chickadee, from literature, correspondence, and my own observations, the modal size was 6 eggs (34.9 per cent). Five eggs comprised 31.8 per cent of the clutches, and the range was 3–9. For the Black-capped Chickadee, modal clutch size was 8 eggs (32.3 per cent of 96 clutches), with 29.2 per cent of all clutches possessing 7 eggs. The range was 2–13. A geographical trend was evident in clutch size, however, with each species having larger clutches at higher latitudes. At the same latitude, Carolina Chickadees produced larger clutches than did Black-capped Chickadees. Modal clutch size for four nests of the *Vandalia* population was 7 (range 6–8), which is nearer the size to be expected for Carolina Chickadees at this latitude.

INCUBATION

Carolina and Black-capped Chickadees. The regular rhythm of sitting characteristic of incubation begins with the laying of the last (or next to last?) egg. At the same time, the flap formerly covering the eggs is no longer used. In both species only the female incubates. The incubation period for Carolina

TABLE 3

CHARACTERISTICS OF ATTENTIVENESS DURING INCUBATION IN BLACK-CAPPED AND
CAROLINA CHICKADEES AND CHICKADEES OF THE VANDALIA POPULATION

Characteristic	Carolina Chickadee	Black-capped Chickadee	Vandalia Population
Minutes observed	843.0	1277.5 ¹	568.0
Percentage attentiveness	77.2	77.5 ¹	68.0
Length of attentive period			
Number	33	10	13
Mean \pm S.E. (minutes)	16.5 \pm 2.45	18.0 \pm 3.62	18.8 \pm 2.31
Length of inattentive periods			
Number	35	11	20
Mean \pm S.E. (minutes)	5.2 \pm 0.66	7.0 \pm 1.07	8.0 \pm 0.85
Feedings of ♀ on nest by ♂ per hour of attentiveness	2.2	2.8	0.6

¹ Includes data from New York.

Chickadees has been reported as 11 days (Bent, 1946), 12 days (Tanner, 1952), just over 13 days, and just over 14 days (Laskey, in litt.). Odum (1942c) has described a case in which infertile eggs were incubated for 24 days. Odum (1941b) summarized published incubation period data for Black-capped Chickadees as from 11 to 13 days; in the one example he actually observed, it was 13 days, 6 hours.

As indicated by Table 3, attentiveness in incubation is similar in the two species. Percentage attentiveness figures, based on my own observations in Illinois plus those of Odum (1941b) for the Black-capped Chickadee (about 960 minutes of observation for New York) and of Brackbill (in litt.) for the Carolina Chickadee (780 minutes in Maryland) indicate that the percentage of time spent incubating is about 75. Attentive periods for the Carolina Chickadee in Illinois and Maryland averaged 16.5 minutes, inattentive periods 5.2 minutes. These figures are similar to those obtained for the Black-capped Chickadee in Illinois. In New York (Odum, 1941b) attentive periods of the Black-capped Chickadee averaged 24 minutes, inattentive periods 7.8 minutes. These differences of a considerably longer attentive period and somewhat longer inattentive period are what one would expect considering the probable differences in temperature between the two latitudes (see Kendeigh, 1952).

When the male approaches the nest, he typically gives a soft version of his whistled song. There is a tendency for the last note of the song to be omitted when thus used as a signal. Sometimes the male merely gives soft *dee-dee-dee* notes. The female may respond by coming to the entrance or by flying out, or she may make no apparent response. Odum (1942a) found that the female

Black-capped Chickadee sometimes gave a soft twitter in response to the male's signal, but I have not detected this answering call in either species.

If called off the nest by the male, the female generally flies to him and begins posturing and giving the beg call. She is usually fed once and the two then fly off. The female often takes the lead in this flight. Once off the nest, the female keeps up a constant begging and is fed repeatedly. While the male is searching for food, she also forages for herself, particularly near the end of an inattentive period.

Often the female does not leave the nest, and then the male usually flies to the cavity and feeds her. He may, however, stay close by and continue calling or merely go away. Whether or not the female ends her attentive period seems to depend partly on the length of time she has been sitting. Occasionally, the female will end an attentive period without the male's presence.

The male may or may not accompany the female when she returns to the nest. The female usually returns in a direct, rapid flight, giving faint *sip* notes. She may perch briefly near the nesting stub or fly straight to it.

Disturbance of a female on the nest may elicit the so-called snake display, which consists of a lunge forward by the bird accompanied by a forced expiration of air causing a kind of hiss. Pickens (1928) has thoroughly described the display, which seems identical in the two species. Some individuals do not give the display, and as Odum (1941*c*) has pointed out for the Black-capped Chickadee, such birds are usually much easier to flush from the nest. Sibley (1955) suggested that the act is a defense against predators. Reactions of other birds, especially House Wrens (*Troglodytes aedon*) upon looking into cavities containing incubating chickadees indicate that the display may also function against competitors for nest sites. The response seems to be to a foreign object entering the nest hole. The display is given, at least to humans, throughout the periods of excavation, nest-building, egg-laying, incubation, and probably brooding. Young birds in the nest give a similar display.

The most usual cause of singing in the female appears to be disturbance at the nest. When a female has been flushed from the nest, she is often hesitant about re-entering and may fly about for several minutes singing. This may be a form of displacement activity or irrelevant behavior. It is conceivable, however, that the songs function as a signal to the male. Sometimes when the female persists in refusing to re-enter the cavity, the male will fly up and look in or even enter the cavity briefly. Usually the female then enters fairly readily, as though the action by the male had a reassuring effect. Another apparent example of displacement activity seen after disturbance at the nest is the bringing of nesting materials, even though nest-building may have been completed several days previously.

The Vandalia population. Although the general outlines of incubation behavior given for the Carolina and Black-capped Chickadees also hold true for the *Vandalia* population, several apparent abnormalities were observed. The one incubation period accurately determined was 14 days, 3 hours, and 33 minutes (± 1 hr., 22 min.). This is longer than all except the longest of incubation periods reported for the parental species. Attentiveness figures showed certain differences compared with the parental species (Table 3). Percentage attentiveness seemed somewhat low, and attentive periods seemed short and inattentive periods long. All of these apparent abnormalities, however, could be merely responses to high temperatures at the rather southerly location. A striking difference, not apparently related to temperature, appeared in the frequency with which the male fed the female on the nest. At all nests except one, the male never visited the nest and often appeared not to know exactly where it was. Repeatedly, males would arrive in the general vicinity of the nest with food and sit for several minutes giving nest signals while the female continued incubation. I know of only one instance in either of the parental species in which the male failed to feed the female on the nest (Black-capped Chickadee: Odum, 1941a).

Perhaps the most noticeably abnormal behavior was that shown by a pair in which the female began what was apparently normal incubation with the laying of the first or second egg. Observations totaling 410 minutes were made on the first, second, third, and fifth days of egg-laying (since seven eggs were laid, incubation would have been expected to begin on the sixth or seventh day). As has been mentioned earlier, the two criteria for the beginning of incubation are the absence of a flap covering the eggs and the presence of a regular rhythm of sitting by the female. No flap was used at this nest at any time. On 26 April 1958, the date of laying of the second egg, a percentage attentiveness figure of 39.5 was recorded. The following day, the female spent 85.6 per cent of 90 minutes on the nest, and on the day the fifth egg was laid, she spent 68.4 per cent of 160 minutes on the nest.

The same nest showed other abnormalities: the pair abandoned after 20 days of incubation (i.e., 14 days after the laying of the last egg). Of the seven eggs, three contained no embryo, one contained a good-sized embryo still several days from hatching, and the others contained much smaller embryos ranging down to a small amorphous mass.

HATCHING AND PARENTAL CARE OF NESTLINGS

In two nests of the Carolina Chickadee observed by Laskey (in litt.) hatching of the complete clutch took somewhat more than 24 hours. Two clutches of the Black-capped Chickadee observed by Odum (1941b) took from 12 to 24 hours. Hatching of one complete clutch of seven eggs at *Vandalia* took

TABLE 4

CHARACTERISTICS OF ATTENTIVENESS DURING NEST LIFE OF YOUNG BLACK-CAPPED
AND CAROLINA CHICKADEES AND CHICKADEES OF THE VANDALIA POPULATION¹

Characteristic	Population	Days after hatching			
		1-4	5-8	9-12	13-16
Minutes Observed	Carolina Chickadee	308	300	300	211
	Black-capped Chickadee	205	—	198	175
	Vandalia population	330	89	423	45
Percentage attentiveness (brooding)	Carolina Chickadee	55.2	25.0	11.7	0.0
	Black-capped Chickadee	71.5	—	9.3	0.0
	Vandalia population	56.2	0.0	7.9	0.0
Mean length attentive period (minutes)	Carolina Chickadee	11.4 (3.0-25.5)	5.3 (2.5-11.5)	8.9 (2.5-15.0)	—
	Black-capped Chickadee	10.5 (1.0-8.0)	—	6.2 (4.0-11.0)	—
	Vandalia population	11.1 (3.0-79+)	—	3.0 (1.0-7.0)	—
Mean length inattentive period (minutes)	Carolina Chickadee	8.2 (3.0-13.8)	16.4 (5.0-33.)	21.0 (3.0-79+)	—
	Black-capped Chickadee	6.6 (2.0-7.5)	—	24.8 (18.0-24+)	—
	Vandalia population	13.6 (1.0-24.0)	—	17.2 (2.5-87+)	—
Feedings by parents per young per hour	Carolina Chickadee	2.6	2.5	2.8	3.8
	Black-capped Chickadee	1.7	—	2.7	—
	Vandalia population	1.4	2.6	2.5	3.7
Percentage of feedings by ♀	Carolina Chickadee	18	25	45	53
	Black-capped Chickadee	24	—	50	—
	Vandalia population	30	—	60	—
Fecal sacs removed per young per hour	Carolina Chickadee	0.07	0.5	0.5	—
	Black-capped Chickadee	0.08	—	0.5	—
	Vandalia population	0.01	0.5	0.5	0.7

¹ Data are for Illinois except for 333 minutes of observation of Carolina Chickadee from District of Columbia (Brackbill, in litt.). Ranges are in parentheses.

19 hours, 33 minutes (\pm 6 hours, 20 minutes). Hatching apparently occurs at any time of the day or night. I have not determined what disposition is made of eggshells, but they are not allowed to remain in the nest. Infertile eggs, however, are not removed.

Attentiveness continues about the same as in incubation for the first three days after hatching (Table 4). Then there is a rapid decline, and about the 11th day brooding is completely discontinued. The rate at which nestlings are fed increases during nest life. As has been pointed out for the Great Tit (Betts, 1955), the feeding rate, based on visits to the nest by the parents,

is not a completely accurate reflection of the amount of food the young receive because more than one item is sometimes brought and the average size of food items increases during nestling life.

Feeding may be almost entirely by the male during the first few days after hatching. The male brings food to the female during her attentive periods and feeds the young directly during inattentive periods. During the early days after hatching the female almost never returns to the cavity with food during an inattentive period, although she may bring food when she arrives to resume brooding. The male rarely feeds the female off the nest after young are present, although she begs frequently during the first few days. When the two meet near the nest with food, there is mutual wing-shivering which is more pronounced in the female. In this situation the male feeds first, the female flying to the hole immediately upon his departure. By the time the female terminates brooding, the sexes share about equally in feeding duties, and by the end of nestling life the female is performing the greater part of the chore.

Fecal sacs are removed by both parents, although there is some indication that this function is performed more often by the male. Often a bird will perch at the hole for several seconds after having fed, evidently waiting for the young to defecate. There is an increase in the frequency of production of fecal sacs with increasing age of the young. That the adults may eat the fecal sacs during the first day or two after hatching is suggested by the extremely low rate of removal during that period. When carrying a fecal sac, the adult appears to take a longer, more direct flight away from the nest than is otherwise the case. It perches higher than the average feeding height and deposits the sac on a limb. Near the end of nestling life, when feedings are very frequent, there may be some tendency for fecal sacs to accumulate in the nest.

Parental care of nestlings by birds of the *Vandalia* population seemed identical to that practiced by the two parental species. This fact is remarkable in view of the anomalous behavior in incubation. For example, one might expect that since the male did not feed the female on the nest (except in one pair), he might also neglect the young. This did not happen, the male assuming an apparently normal share of the duty.

Length of nest life appears to be about 16 days (Laskey, in litt.; Bent, 1946; Odum, 1941c). The time required for a brood to leave the nest has been reported as 40 minutes for seven Black-capped Chickadees (Odum, 1941b). Four Carolina Chickadees in the laboratory fledged in a period of 100 minutes. In both species, fledging generally takes place in the morning.

Hatching success (eggs hatched per eggs laid) is on the order of 95 per cent for the Carolina and Black-capped Chickadees, and fledging success (birds fledged per eggs laid) is between 70 and 90 per cent. For the *Vandalia*

population, hatching success was no more than 65 per cent, fledging success no more than 43 per cent. Both of these figures are significantly lower than those for the parental species. The low rate of successful reproduction resulted from infertility and retarded development of eggs, destruction by House Wrens, and destruction by an unknown predator.

BEHAVIOR AND DEVELOPMENT OF NESTLINGS

No systematic observations were made during early nest life. The scattered data obtained suggest no differences from early development of the Black-capped Chickadee as reported by Odum (1941*b*, 1943) and Johnston (1941). The following comments pertain to a brood of four Carolina Chickadees hand-reared in the laboratory from the thirteenth day on.

13th day. By this time the young are well-grown and well-feathered, with only a few traces of down. They beg by gaping and calling the usual beg call of females and fledged young rather than the high-pitched twitter of younger nestlings. The sight of the wiggling mealworm evokes the beg; however, the young also beg when they are hungry and we are not close by. The young are not dextrous with the worms and cannot swallow them unless the worms are put well down in the mouth, headfirst. The young make no effort to get out of the nest through an opening cut on a level with it. There is a rotation in feeding through the actions of the young. Birds which are not hungry do not beg, and the hungrier birds are more active in moving to the top of the nest. Defecation occurs shortly after feeding, although not after each feeding. The young bird puts its head down and its tail up pointing toward the entrance (or at least away from the center of the nest) and expels a gelatinous sac which is white with a black-brown inner tip. After being fed to satiation, the young sleep. The young sometimes hiss at the movement of an object toward them. This response is present at least as early as the tenth day.

14th day. Three of the young now feed actively, lunging at the forceps. Any tapping or jarring of the nest causes the birds to assume a crouched, immobile posture. They also do this when removed from the nest. This freezing reaction apparently begins about the seventh day and occurs in response to stimuli which previously would have produced begging. Begging behavior, besides being elicited by the sight of a worm, also is elicited by pressure. When the observer felt in the nest, trying to remove a bird, the ones not being sought begged vigorously. The young birds also now beg at the sight of the forceps even if the forceps contain no worm. After a freezing reaction, if one bird resumes begging, all start in. Usually after being fed until full, they sleep. They may, however, preen, apparently using the preen gland.

15th day. Fecal sacs are now decidedly less gelatinous. Each bird ate about 80 mealworms on this day and discharged 10-14 fecal sacs. These are usually discharged one to a feeding period, immediately after the 1st or 2nd mealworm. The birds now usually beg only when the observer is in the cage. The sound of an airplane overhead induces freezing, as does also the sounds of people close by and replacing the cover over the cut opening in the stub. Some wing-flapping occurred on this day, and there was some interest in looking out of the hole. After the last feeding at 7:30 PM, one bird jumped out of the cut opening, hung on the side of the stub, and discharged a fecal sac. The bird was returned to the cavity and remained there.

16th day. 7:50 AM. The bird marked with blue flew out. It flew at the highest part of the cage, finally coming down at 8:15 to accept one worm. By 9:10 another bird

was out. Yellow, the third bird, came to the opening several times, then backed into the cavity and shivered its wings. Finally, at 9:25, it flew out. Red, the fourth bird, perched on the rim of the opening, gradually getting farther and farther outside. It looked from side to side and begged. After five minutes of this, it flew out a short distance, climbed up the wire walls of the cage and then began flying around as the others were doing. One or more of the birds when perched on the wire side walls or ceiling hung upside down, bat-like, perhaps because of weakness of leg muscles. By 10:30, feces were no longer enclosed in sacs at all. Jarring of their perch, now that the birds were out of the nest, no longer produced a freezing response.

Observations of caged Black-capped Chickadees over the same period of development detected no appreciable differences in the two species.

PARENTAL CARE AND BEHAVIOR OF FLEDGLINGS

When young birds have just fledged, the adults lead them away from the vicinity of the nest. The young may be taken to a distant part of the territory or even off it. The family group is subject to attacks from pairs which are still nesting, but the nesting pairs seem not to be particularly successful in their efforts to drive the family groups away.

The adults seem to direct the movements of the young, perhaps by the use of whistled songs. At least, singing by both parents is frequent during the early fledgling period. When the group is disturbed by humans, the pair, particularly the male, scolds vigorously. Odum (1941*b*) has described an injury-feigning display, similar to that of shore birds, performed by parent Black-capped Chickadees when the young gave the distress call. I have not seen this display in either species. The begging posture and notes of the young are identical to those of the adult female during the early part of the nesting cycle. Disturbances cause the adults to interrupt feeding of the young.

Within a week after fledging, young are able to forage for themselves to some degree. They may be fed by the parents for another two weeks or so before the family group breaks up.

The following comments are based on observations of four hand-reared Carolina Chickadees, but appear to apply equally well to a brood of Black-capped Chickadees which were studied in the laboratory during the same period of development.

1st day (day of fledging; 16 days after hatching). The young spend considerable time preening. It is difficult to induce begging. One bird took a piece of hamburger too big to swallow and put it under its foot in the manner of an adult. The birds drank water after being set on the rim of the container. By 6:57 PM all were asleep. Three slept sitting normally on a perch, but with breast feathers well-fluffed and head bent down. The fourth slept with its head under its wing from top and back in the manner of an adult.

2nd day. General behavior was similar to the first day, but begging was more frequent. Mean weight 9.7 grams (9.5-10.1).

3rd day. One bird grasped a piece of food too large for it strongly in one foot and

proceeded to eat it. Some of the birds will come to the observer for food. Some will pick up and eat small mealworms laid down beside them. None of the birds can land well on perches yet. Mean weight 10.0 grams (9.6–10.4).

4th day. All were much wilder this day, perhaps because of the calls and actions of the adult Black-capped Chickadee in the adjoining cage. One young bird often begged from another, even though the second may have had no food. The birds appeared curious, pecking at their perches, their own or another bird's feet, or their plumage.

6th day. Mean weight 9.8 grams (9.7–10.1).

7th day. This day all birds would fly down to pick up worms they had dropped. Also they would feed themselves from the container of worms when the observer was not present. Two birds gave a kind of *sotto voce* call, resembling somewhat the song of a White-eyed or Warbling Vireo (*Vireo griseus* or *V. gilvus*), but soft and not whistle-like. Begging is less frequent and also there is little sleeping during the day.

10th day. One bird gave the *dee-dee-dee* general call note for the first time. This occurred when the observer had removed one of the two remaining birds to a different cage. Sun-bathing was observed in one bird.

In both species I have found instances of what appeared to be re-nesting following some kind of interference with the first nesting. I have never found good evidence of second broods in either species. Odum (1942*b*) in two seasons in New York detected one second brood in 10 nesting pairs of Black-capped Chickadees in a season cooler than usual and three second broods in 13 nesting pairs in a season warmer than usual. It seems clear that second broods are infrequent in both species.

TIMING OF REPRODUCTIVE EVENTS

The date of laying of the first egg was obtained from my own observations, literature, and correspondence. In nearly every case, this date had to be established indirectly by allowing one day for each egg laid, 13 days for incubation, and 16 days for nest life. Approximations of first-egg dates were made from the following kinds of information: daily schedule of laying, date of fresh complete clutch, date of hatching, and date of leaving nest. The sample for Carolina Chickadees included 42 dates from 29.0 to 39.8° N. Lat., that for Black-capped Chickadees 27 dates from 39.8 to 46.0° N. Lat. The data were so variable that no firm conclusions could be reached, other than that both species tended to begin laying 3½–4½ days later for each degree of latitude northward. Using the best data from 38.5–40.5° N. Lat., the date for laying of the first egg ranged from 24 April to 15 May for Carolina Chickadees (N = 6) and 14 April to 20 May for Black-capped Chickadees (N = 9).

Estimates of timing of other events in nesting can be obtained for either species as follows: excavation and nest building begins about 20 days previous to laying of the first egg; hatching occurs about 13 days after laying of the last egg; young leave the nest about 29 days after laying of the last egg; and young reach independence 45–55 days after laying of the last egg.

The mean date of laying of the first egg for seven pairs of birds of the

Vandalia population (about 39° N. Lat.) was 19 April (median 25 April, range 8 April–2 May; six records for 1958, one for 1959). The earliest date of observed excavation was 27 March, the latest 17 April.

MISCELLANEOUS ACTIVITIES

Other than those already considered, activities engaged in by chickadees involve feeding, roosting, preening, resting, drinking, bathing, sun-bathing, and avoidance and scolding of enemies. Some of these are discussed elsewhere in this paper. In this section only preening, bathing, and sun-bathing will be considered.

Preening appears not to differ appreciably in the three populations. The following observation was of a bird of the Vandalia population:

(The bird) wiped bill, then preened around neck, letting wings lie rather limp. Then preened right wing, then scratched right side of head, leg coming up behind wing. Then preened right side of tail, spreading and raising it and pulling it to the right. Then preened around preen gland. These actions were then repeated on the left side in approximately the same order. Bird would wipe bill on limb occasionally. Bird then defecated and moved to a lower branch. It went through many of the same motions, scratching even more vigorously, then also preened around ventral apterium. Bird faced east, was in open, but was not in direct sun (there being none).

Less extended observations of the bathing of Carolina Chickadees suggest that the actions are similar to those noted for the Black-capped Chickadee on 19 November 1958:

A chickadee which had been looking for food flew to ground at river's edge, then flew to edge of water and, sitting in it, bathed. It stayed for about one minute and bathed by bending over and shaking head back and forth, at the same time spreading wings. Would pause several seconds between each bend-over. Finally flew up, fluffed feathers, flew further and began to preen.

Odum (1942*b*) has stated that in winter, when there was no open water, birds were observed "snow-bathing." The birds would fly down to where the sun shone on the snow and would flutter around on the moist surface. There are no reported instances of snow-bathing in the Carolina Chickadee, perhaps because open water is nearly always present and snow rather infrequent over most of the range of this species.

Sun-bathing appears not to be previously reported in Black-capped and Carolina Chickadees, but it occurs in both. I have seen it only in young birds, from five days after fledging to one or two months. The four examples of sun-bathing observed, two in each species, all occurred on sunny days following one or more cloudy ones. The following description is for the Black-capped Chickadee, but the actions seem identical in the Carolina Chickadee.

On 26 June 1958 the bird perched at the top of cage about 1:00 PM in sun, spread one wing, then spread the other, then as it sat there, other feathers were ruffled and the head slowly fell forward (beak pointing down). At maximum intensity, the wings were spread, plumage lax, and right eye pointing toward sun.

VOCALIZATIONS

The following discussion is based on Odum's (1942*b*) analysis of the Black-capped Chickadee.

Whistled song. This vocalization is similar in the two species, consisting of high-pitched clear whistles. The whistled song of the Carolina Chickadee is typically four-noted, *fee-bee-fee-bay*. Nearly always when the song is heard at close quarters, the first and third notes are lisped, so that *tsee-bee-tsebay* is perhaps a closer rendering. Other transcriptions of it are *sufee-subee* (Bent, 1946) and *se-bee-se-bu* (Tanner, 1952). The song is generally stated to be higher pitched than that of the Black-capped Chickadee, but I am not sure that this is true. Saunders (*in* Bent, 1946) observed that the second and fourth notes of the song are pitched about the same as the two notes of the Black-capped Chickadee, B and A or A and G in the highest octave of the piano, with the first and third notes higher or lower. A frequent version in Illinois is B-B flat-B-A. The quality of the song, particularly the first and third notes, differs from that of the Black-capped Chickadee in being thinner, lisped, and more tremulous. The phrasing is characteristic, with one or both of the first two notes drawn out and the last two rapidly given.

Variations include three-noted songs which sound like *fee-bee-feeep* and six- or more-noted songs, which may be *fee-be-fee-be-fee-be* or *febay-febay-febay*. These are given as occasional variants by birds which also sing the four-noted song. On the Big Muddy River south of Murphysboro (Jackson County), Illinois, many or all of the birds sing *fee-be-febzz*, the last syllable being much more buzzy or burred than is usually the case.

In Black-capped Chickadees, the song is characteristically two-noted, *fee-bee*, pitched B-A or A-G. A variation of this song is three-noted, *fee-be-bee* or *fee-bee-ee* (Odum, 1942*b*). Dawson and Bowles (1909) stated that *P. a. occidentalis*, in contrast to *P. a. septentrionalis*, sang a three- or four-noted song pitched C-C-C or C-C-C-A. Lumley (1934), in reporting a similar song, felt that it resulted from individuals imitating the song of the Mountain Chickadee (*P. gambeli*). Bagg (1958) reported what appears to be a local variation, in which birds of Martha's Vineyard sang a monotonal two- or three-noted song. A similar song has been reported from the Gaspé Peninsula (Bagg, 1958) and in Ontario (Lawrence, *in litt.*).

In the area around Vandalia, five apparent classes exist with regard to whistled songs: those which give only Carolina songs, those which give only Black-capped songs, those which give only songs outside the normal range

of variation of either species, those which give both unusual and Carolina songs, and those which give both unusual and Black-capped songs. Most of the unusual songs were of the general type *fee-be-deekee-deekee*, usually pitched B-A-BB-BB in the highest octave of the piano. Variations were frequent, including omission of the first portion (*deek-ee-deek-ee-deek-ee*), variations in length of the second portion, and changes in inflection or phrasing (*fee-be-tswee-tswee*, *fee-be-deekit-deekit*, *fee-bee-deet-dee*, *see-bee see-beesebee*, *fee-be-deup-deup*). These vocalizations were given both by birds that gave only unusual whistled songs as well as those which gave Carolina or Black-capped songs. A second unusual song type may have been restricted to those which gave only unusual songs or those giving both unusual and Black-capped. This was of the general form *fee-fee-deet-dee*, usually pitched G flat-G flat-B-B or B-B-A-A. Two other unusual types of whistled songs were *sweet-towee-towee* (and variations) and *fee-a-be-fe-be*. Neither of these was encountered more than a few times.

In the contact zone of eastern Missouri, most of the vocalizations were of the *fee-bee-deekee-deekee* type. A variation of this, *fee-deet-dee* or *fee-sbee-sbee-sbee*, rarely heard at Vandalia was fairly frequent. Another type, not heard at Vandalia, was given by two birds in Missouri and could be written as *fee-bee-bay*. It consisted of three notes each on a different pitch and given in no apparent order (high, medium, low; medium, low, high; etc.). It is possible that this may be a normal but rare vocalization of the Carolina Chickadee, for Saunders (*in Bent*, 1946) recorded it in that species. It is interesting that this song apparently duplicates one of the normal whistled songs of the Mountain Chickadee (see Saunders *in Bent*, 1946).

The whistled song is generally given by the male. Juveniles may sing about the time of the post-juvinal molt. The annual trend in frequency of the whistled song suggests a connection with reproduction. The song is rarely given from October through January, but there is a sharp increase in February. The peak frequency is reached sometime in April—somewhere near the period of egg-laying—in Illinois. There is a gradual decline to October, with perhaps a slight recrudescence in late August or early September. Functions of the whistled song appear to be proclamation and defense of territory and maintenance of contact between members of a pair. In the second function, it appears to be used at greater distances than the general call note.

Signal song. The signal song is like the regular song, but much softer, of a rather ventriloqual quality, and often reduced by one note. It functions in announcing to the female the approach of the male to the nest. Signal songs of males of the Vandalia population tended to be soft, shortened versions of the *fee-be-deekee-deekee* whistled-song type (Examples: *fee-bee-deet-dee*, *fee-ee-deek-ee*, *fee-deek-ee*).

General call note. The general call note is the *chicka-dee-dee-dee* call which gives the birds their name. Considerable variation exists in the number of *dee*'s and in the presence, absence, or repetition of the *chicka* portion. A high, hard *didit-didit*, somewhat resembling a call of the Downy Woodpecker, appears to be a variation of the general call note without special significance. Tanner (1952) has stated that the general call note is higher-pitched, thinner, and more rapidly given in the Carolina Chickadee, but I am often unable to distinguish the species on this basis. The call is used by both sexes to announce the position of the calling bird to its mate or, in winter, to other members of the flock.

Fighting and dominance notes. I have not been able to separate clearly the fighting note and the dominance note of Odum (1942a) for either species. The first Odum has described as a sputtery, high-pitched, beady *chick-a-dee* or *chit-chit-chit* given during spring conflicts between pairs and during the chasing and fighting phases of territorial defense. The second was described as a throaty *che-lup* or *che-up-che* which is given most often by aggressive males. The note was said to be a vocal threat used when birds come close together or one bird chases another.

As nearly as I can tell, a kind of falsetto *chick-a-deep* or *chick-a-deep-chick-a-deep* has been my rendition of the note that would correspond to the fighting note. A note I usually rendered as *deedle-up* appears to be the equivalent of the dominance note. These notes are similar and a variety of intermediates seem to exist. All of the notes are clearly related to aggressiveness. The connection between aggressiveness and courtship may be suggested by the fact that a male Carolina Chickadee gave the *deedle-up* note just before treading its mate.

Begging note. My most accurate transcription of this call is *che-che-weweweup*. The call is variable and difficult to syllabify. The note is given by young from just before fledging throughout their period of dependence and by the female of mated pairs from nest building through incubation and somewhat beyond. At full intensity, the begging bird crouches and shivers its wings rapidly.

In most cases, there appeared to be no difference in this call between the three populations. The female of one pair of Black-capped Chickadees, however, began about the ninth day of incubation to give a beg call which I recorded as *chee-chip*. This is similar to the version of the begging note reported by Odum (1942a): *tee-ship* or *tee-chip-she*. Other female Black-capped Chickadees gave the *che-che-weweweup* call throughout incubation.

Other notes. Odum (1942a) also recognized for the Black-capped Chickadee a scolding note, an alarm note, a contact note, a flight note, a warning note, and the hissing note of the snake display, all of which I have heard in

the Carolina Chickadee or in both species. All seem identical in form and function in the two species and in the Vandalia population. Other notes listed by Odum, I have either not heard or failed to recognize in the Carolina Chickadee. Additional notes heard by me which appear not to be distinguished by Odum are the following: a *ticket-ticket* or *dickit-dickit-dickit* which appears to be used by both species before or after flock movements; the *sotto voce* song of young Carolina Chickadees fledged eight days.

DAILY ACTIVITY

The awakening time of chickadees of all three populations seems closely related to sunrise in females throughout the year and in both sexes during the winter. During the breeding season, however, males seem to awaken and become active 30 or more minutes before sunrise. The time of roosting is variable, with earlier roosting with respect to sunset being the rule in winter and perhaps early spring and on cloudy days. Roosting may be latest when a pair is feeding young in the nest. I have at that time found female Black-capped Chickadees active 16 minutes after sunset. By the time the female is roosting in the nest cavity, the male has begun retiring later as well as arising earlier than the female. The early morning period often is one of relatively frequent singing on the part of the male, but the twilight period is nearly silent. In Illinois, the period of activity for the male is about 15 hours during May and about 9 hours during January. For the female, it is somewhat more than 14 hours during May and about 9 hours during January.

WEIGHT

In an analysis of weights of the two species of chickadees, four trends are noticeable. First, both species show a trend of increased weight from south to north. For example, the mean weight of male Black-capped Chickadees in Ohio (41.5° N. Lat.) from April to September appears to be about 11 grams (Baldwin and Kendeigh, 1938), whereas during the same period in Ontario (46° N. Lat.) males weigh more than 12 grams (Lawrence, 1958). A similar comparison can be made for Carolina Chickadees using weights from Illinois (Table 5) at an average latitude of about 38.5° N. Lat. where males in the winter average about 10.5 grams and females about 9.6 grams and weights from Ohio (Nice, 1933) where males average 11.2 and females 10.1 grams. At the same latitude, Black-capped Chickadees appear to be slightly heavier than Carolina Chickadees.

Within a species, males are considerably heavier than females (Table 5; see also Odum, 1943; Hartman, 1955; and Norris and Johnston, 1958). This difference diminishes during the egg-laying season. A fourth trend is seasonal, with birds being heavier in winter and spring, lighter in summer and fall (Lawrence, 1958; Odum, 1943).

TABLE 5
WEIGHTS (IN GRAMS) OF CAROLINA CHICKADEES IN ILLINOIS
(AVERAGE LATITUDE ABOUT 38.5°N.)

Month	Males		Females	
	Number	Mean \pm S.E.	Number	Mean \pm S.E.
January	5	10.8 \pm 0.25	6	9.7 \pm 0.25
February	4	10.7 \pm 0.43	4	10.1 \pm 0.32
March	4	10.4 \pm 0.34	4	10.1 \pm 0.34
June	—	—	1	10.0
November	2	10.0	5	8.9 \pm 0.38
December	3	10.1 \pm 0.02	8	9.7 \pm 0.18

Besides varying with species, latitude, sex, and season, weight in the Black-capped Chickadee also varies with time of day, according to the data of Lawrence (1958).

SUMMARY

The life history of the Carolina Chickadee was studied from October 1954 to November 1959. During the same period observations were made on Black-capped Chickadees and a population believed to be composed at least partly of hybrid birds. Most of the field work was in Illinois, with that for the presumed hybrid population confined mainly to the contact zone near Vandalia.

The three populations were found to be similar or identical in most respects. In winter, chickadees of all three populations tend to occur in flocks, the mean size of which is three to four birds in Illinois. Home range size appears to be related to food supply and is on the order of 35 acres at the latitude of central Illinois. Chickadee flocks tend to occur in temporary feeding parties. In spring and fall these parties may include migrant warblers and vireos; in winter, the most frequent associates of chickadees are Tufted Titmice, Downy Woodpeckers, Golden-crowned Kinglets, and White-breasted Nuthatches.

Pair formation apparently begins in the flock and is a gradual process. Members of a nesting pair tend to remain together during the winter and, if both survive, to nest together the following season. Excavation and even nest-building may be begun at several locations before the pair finally concentrates on the site which is actually used. Carolina and Black-capped Chickadees almost invariably excavate their own cavity, with both sexes participating. In the Vandalia population, excavation appeared nearly confined to the female. Nests in Illinois are usually of moss overlain by fine bark strips and lined with fur. Gathering of nesting materials and nest building is almost entirely by the female. Eggs are laid one each day in the morning. A geographical trend in clutch size exists, with Carolina Chickadees tending to have larger clutches at any given latitude than Black-capped Chickadees. Date of laying of first egg also varies geographically, tending to be 3½–4½ days later for each degree of latitude northward.

Incubation is by the female and is begun with laying of the last or next to last egg. The incubation period appears to be about 13 days. Attentiveness is about 75 per cent for the Carolina and Black-capped Chickadees. Attentive periods in Illinois average about 15–20 minutes in length, inattentive periods 5–8. In the two species, the incubating female is fed by the male about two to three times per hour of attentiveness. During

inattentive periods the female gives a begging display and is fed repeatedly by the male. Among apparent abnormalities observed in the Vandalia population were a nearly complete lack of on-the-nest feedings of the female by the male, initiation of incubation with the laying of the first or second egg (in one pair), and a low rate of hatching and fledging of young.

Hatching of the complete clutch in all three populations requires about 12-24 hours. The percentage of time spent brooding is about the same as that spent incubating for the first three days after hatching; then there is a rapid decline until brooding is completely discontinued about the 11th day. At first, feeding of nestlings is almost entirely by the male, but by the end of nest life, the female has assumed the greater share of this duty. Length of nest life is about 16 days. Development of young Carolina and Black-capped Chickadees studied in the laboratory from the 13th day on seemed essentially identical, as did the behavior of fledglings during the first 10 days after leaving the nest. By about 7 days after leaving the nest, young are able to forage for themselves to some degree, but may remain with the parents for another two weeks before the family group breaks up.

The two species have an extensive and similar vocabulary. Small differences exist in the whistled song, the signal song, and to some degree the general call note. Many birds of the Vandalia population gave whistled songs and signal songs far outside the normal range of variation of the two parental species.

Miscellaneous activities, such as preening, bathing, and sun-bathing, appear to be similar or identical in the three populations. The pattern of daily activity is similar, with awakening time related fairly closely to sunrise in the female. The male tends to arise earlier and retire later than the female in the breeding season. Within each species, weight varies with latitude, sex, season, and time of day. With other conditions equal, Carolina Chickadees appear to weigh slightly less than do Black-capped Chickadees.

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DEPARTMENT OF BIOLOGY, WESTERN MICHIGAN UNIVERSITY, KALAMAZOO,
MICHIGAN, 10 JANUARY 1961

NEW LIFE MEMBER

G. Stuart Keith, Associate, Department of Birds, American Museum of Natural History, is the newest Life Member of the Society. Mr. Keith received his Master of Arts Honors Degree in Classics at Oxford in 1955. His chief ornithological interests are in behavior, systematics, photography, and conservation. His two papers have recently appeared in *Natural History Magazine* ("The Dances of the Japanese Crane") and in *Tori Magazine* ("Winter Birds of Hokkaido, Japan"). He is also a member of the London Natural History Society, the Tori Society of Japan, the International Council for Bird Preservation, the AOU, and is at present a Director of the Alberta Wildlife Foundation.

The achievement of which Mr. Keith is most proud is his breaking of Roger Peterson's record for the greatest number of birds seen in North America in a single year. Dr. Peterson saw 572 species in 1953, and Mr. Keith saw 594 in 1956.

